

A homeland or hostland? The power and challenges of genetic studies on Austronesian's expansion

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(Abstract)

The puzzle of Austronesian speaker's place of origin and routes of expansion has long fascinated linguists and archeologists. Although enormous genetic studies have dealt with this issue over the past decade, only a few focused on Taiwan's position. In this paper we review the genetic data and examine Taiwan's unique position in Austronesian's expansion. It's our conviction that most of Taiwan aborigines (except the Ami), originated in central or southern China, moved to Taiwan a few thousand years ago and remained in Taiwan for a long time. The Ami was probably moving in separately, and kept contacting with other populations of Southeast Asia islands after they have settled in eastern Taiwan. While genetic studies appear to be powerful in tracking the relevant populations' relations, we examine also the challenges they have faced.

Taiwan in Austronesian expansion: one-way ticket or round-trip?

Today, twelve groups of Austronesian speakers (AN) have been officially recognized by Taiwanese government. The total population of Taiwan aborigines is only 450,000, or 0.16% of the entire AN populations.

The small population of Taiwan aborigines does not mean that they have low diversity in languages and cultures. In terms of languages, for example, Linguist Blust (1999) classifies the 1,200 AN languages into ten subgroups, of which nine are solely spoken in Taiwan and the tenth subfamily language (Malayo-Polynesians) widely dispersed from Madagascar to Easter Island, holding a high similarity which suggests a recent common origin. As to the cultures, both patrilineal and matrilineal systems coexisted on the small island (Hsu, 1991).

The linguistic evidence is frequently used to support the 'express-train' model, according to which Polynesian ancestors moved to Taiwan from southeastern part of Asia (nowadays southern China) and then rapidly migrated en route the Philippines to the Pacific islands without significant admixture with indigenous Melanesians (Papuan) (Gray and Jordan 2000; Diamond 1988, 2000). Archaeological evidence suggests that western Polynesian islands (Fiji, Futuna, Samoa, Tonga) were settled 2,100–3,200 BP by peoples belonging to the so-called Lapita culture, a cultural

complex of pottery and agriculture originated about 6,000 BP in China/Taiwan, and quickly dispersed like an express-train to the Pacific islands (Bellwood 1985, 1995). In this express-train model, Taiwan is regarded as the first stop to stay for sometime and then emigrated to Southeast Asia and Oceania, presenting what Diamond (2000) described “a gift to the world” — the homeland of further AN expansion.

While the express-train model may sound a fascination, it also raised debates. Among some other different models proposed, the ‘entangled-bank’ and its follower ‘slow-boat’ model lie at the opposite end of a spectrum (Hurles et al. 2003). The slow-boat model is modified from the entangled-bank model (Terrell 1986; White *et al.* 1988), suggesting a strict Melanesian origin of the Lapita culture and long history of cultural and genetic interactions among ANs and PAUs. Supported by some archeological evidences, proponents of the slow-boat model consider the broad triangular area formed by Taiwan, Sumatra, and Timor as the homeland of ANs (Oppenheimer & Richards 2001). Since the first arrival of PAUs at least 50,000 years ago, the populations in this enormous insular array kept more or less in touch with one another. The slow-boat model argues not only for a proximate Polynesian origin within Wallacea, but also for the first station of AN expansion in island Southeast Asia, rather than Taiwan. The position of Taiwan in this model is totally different from that of the express train model — a hostland, instead of the homeland.

While genetic data had been believed to be a powerful tool to solve the puzzle of blood ties among related populations, the mutually conflicting findings speaks to the necessity of interdisciplinary evidence. In this paper we first portray the genetic vista on AN expansion, and then use archaeological and cultural evidence to probe Taiwan’s role in AN expansion.

Perspective of classical markers, HLA, and autosomal genetic markers

The genetic studies of Taiwan AN populations have long attracted the attention of medical doctors and geneticists. Many classic markers, such as ABO, Rh, MN, Gm, had been tested as early as 1940s. The earlier studies pointed that Taiwan AN populations affiliated commonly with East Asia, corresponded with the northern origin (Chou 1959; Huang 1964, 1970; Huang & Sheen 1966; Nakajima *et al.* 1967, 1971; Nakajima & Ohkura 1971). However, a study of 21 classic markers among the Truko found affinities primarily with the Philippines and Thailand and to a lesser extent with south China and Vietnam, corresponded with southern origin (Chen *et al.* 1985). Lin & Broadberry (1998) studied multiple RBC polymorphic markers among nine Taiwan AN populations, and concluded a scenario of several migratory events from multiple sources in both East Asia and Southeast Asia.

Two other serum proteins studies showed conflict results: significant heterogeneity for serum complement proteins was observed among Taiwan ANs, supporting a scenario of multiple sources in northern and southern origin (Umetsu *et al.* 1994), but high frequencies of some orosomucoid alleles that were more common in East Asians than in Southeast Asians inclined northern origin (Umetsu *et al.* 1995).

The Human Leukocyte Antigen (HLA) is the major histocompatibility antigens system found on all cells of the body that determine white blood cell types. HLA tissue types are used to match donated organs or bone marrow with transplant recipients. Therefore, people from the same origin are more likely to inherit the same HLA type. The HLA system is highly polymorphic than RBC so as to become an important tool to study the relationship between populations since 1970s. In 1991, the HLA allele frequencies of worldwide populations had been collected such that international comparison becomes possible (Imanish *et al.* 2002). Shaw Chen-kuang *et al.* first typed HLA of Taiwan AN in a single label in 1999, and found Javanese highly close to Taiwan ANs. All East Asian populations formed another cluster quite apart from Taiwan AN and Javanese. Professor Marie Lin and her associates (2000) studied 9 Taiwan AN populations and 1 highly hybrid population (Pazah) and compared the allele frequencies of Asians, North American Indians and Oceanians. They found Taiwan AN populations closely related to the Oceanians with Ami closely linked with PNG Highlanders, Yami showing affinity with Javanese, and the rest of Taiwan ANs forming a tight cluster. A similar pattern of linkage repeated while the Ivatan samples from the Batan Island of the Philippines were added and reanalyzed. Taiwan AN populations were grouped into three clusters: Ami showing affinity with PNG Highlanders and Australian Aborigines, Puyuma and Yami showing affinity with Ivatan, and Atayal, Saisiat, Bunun, Tsou, Paiwan, Rukai forming a tightly cluster (Chu *et al.* 2001). (See Figure 1.)

The microsatellite is a repetitive stretch of short sequences of DNA, a genetic marker frequently used to track inheritance in families. They are short sequences of nucleotides (example: ATCG) which are repeated over and over again a number of times in tandem. They are also called Short Tandem Repeats (STR). Again, people from the same origin will have higher probability to inherit the same repeat number of each microsatellite marker. Microsatellites have been widely used to study the genetic relationship among human populations since 1980s. Chu *et al.* (1998) studied 4 Taiwan AN populations (Ami, Atayal, Paiwan, Yami) along with 22 minorities in China, and few other populations worldwide. The cluster analysis based on 30 microsatellites markers found that the four Taiwan aborigines shared the same root with Deang (southwest Yunnan, Tibeto-Burman) and Jingpo (west Yunnan, Tibeto-Burman). The cluster cannot be used to infer the origin because Deang and

Jingpo are located in the middle of East Asia and Southeast Asia (Figure 2). Besides, Wei *et al.* (1999) and Lee *et al.* (2002) studied other microsatellite markers merely among Taiwanese AN samples without comparing the relationship between Taiwan AN populations and other relevant populations.

In sum, the above studies of traditional genetic markers suggest that Taiwan AN populations could be originated in the south (RBC, HLA), or from multiple areas (RBC, serum proteins). However, the frequency distribution can only be used to find the similarity between populations and cannot be used to trace the human migration history (Wei *et al.* 1999:341). Due to its conservative function in immune reaction, the HLA types between chimpanzee and humans cannot be clearly divided into two separate clusters. Although chimpanzee and humans have split for long in the history of evolution, they still share the similar HLA types (Ayala, 1995). In other words, the HLA type itself cannot be used to trace the migration of human populations while its frequency is useful to test the similarity. Therefore, the similarity between Ami, PNG Highlanders and Australian Aborigines in Chu *et al.* study (2001) is too early a convincing result to explain the migrations between groups.

Perspective from Y-chromosome

In recent years, genetic anthropologists studies of Y-chromosome (Underhill *et al.* 2001) and mitochondria DNA offered more direct and precise evidences for human dispersal (Kivisild *et al.* 2002). Theoretically, autosomal lineage recombines each generation, while Y-chromosome and mtDNA lineages do not. Therefore, an individual cannot trace back to any certain ancestor on the basis of autosomal lineages. Quite contrarily, the Y-chromosome and mtDNA have unambiguous paternal or maternal ancestor. The absence of recombination helps to sustain the lineage in a relatively small and stable population so as to generate population-specific markers. Y-chromosome and mtDNA lineages can be considered as alleles from a single locus that occurred in an ordered time series in human history, each of which might mark the footprint of a unique migration event.

Today many genetic research teams worldwide used Y-chromosome to study AN expansion, and some of them recruited Taiwan AN samples (Su *et al.* 1999, 2000; Kayser *et al.* 2000, 2001, 2006; Underhill *et al.* 2000, 2001; Capelli *et al.* 2001; Hurles *et al.* 2002, 2005). Su *et al.* (1999) genotyped Y-chromosome lineages among 5 Taiwan AN populations (Atayal:24, Yami:8, Paiwan:11, Ami:6, Bunun:9) and many Asian populations and found that the Y-chromosome lineages of southern East Asian populations are much more diverse than their northern counterparts, illustrating that southern East Asia was the first settlement of modern humans of East Asia. By reanalyzing the same set of data, they provided a breakthrough result, opposing the

direct relationship between Taiwan ANs and Polynesians (Su *et al.*, 2000). According to their analyses, it is evident that the Taiwan AN populations on one hand, and the Micronesians and Polynesians on the other, carry two different subsets of lineages found in the extant southern East Asians. Nearly none of the Y lineages found in Taiwan appeared in Micronesia and Polynesia: O-M122, O-M119, O-M95 are absent in Polynesia and comparatively rare in Micronesia, but common in Taiwan. Likewise, lineages C-M130, DE-YAP, F-M89* are present exclusively in Micronesia and Polynesia, but rare in Taiwan. The divergence of genetic distance between Taiwan ANs and Polynesians is as twice great as the divergence of either population groups from southern East Asians. This finding led Su *et al.* to postulate that Southeast Asia provided a genetic source for two separate migration, one toward Taiwan and the other heading eastbound to Polynesia through island Southeast Asia. In other words, the distribution of Y-chromosome supports a northern origin.

Su *et al.*'s paper raised many criticisms from linguistics and anthropologists. Too few of samples size of each Taiwan AN populations is among the critiques the most common (Chen and Hsu 2001; Li 2001; Reid 2001). A completely homogeneous O-M119 distribution (100%) of the Ami may be a bias as only six Ami individuals were genotyped. Besides, since no samples from the Philippines were tested, the results become inconclusive for the connection between Taiwan and Southeast Asia.

With more information of Y-chromosome lineages becoming available recently, the Ami turned to be the most heterogeneous among the Taiwan AN populations. Capelli *et al.* (2001) genotyped 262 Taiwan AN individuals (Paiwan:53, Bunun:50, Atayal:50, Ami:53, Yami:40) along with the samples from Southeast Asia, Melanesian, and Polynesian. Data of the Philippines were for the first time included in this study. While the other four Taiwan AN populations kept highly homogeneous with O-M119 more than 70%, Ami showed heterogeneous distribution on O-M119 (43%) and O-M122 (46%). The difference between Ami and other four Taiwan AN populations tends to imply different stories of migration. Interestingly, the difference between other four Taiwan AN populations and insular Southeast Asia and Oceania populations was still significant, but the Philippine samples share identical Y-chromosome lineages with the Ami, but not with the Yami. This result abridges Taiwan AN populations with insular Southeast populations. We calculate the genetic distance between Ami and the Philippines and found it less than a half of non-Ami Taiwan AN populations to Ami or the Philippines respectively (Table 1). Given this breakthrough, it seems plausible to revise Su *et al.*'s conclusion: as most Taiwan AN populations remained in Taiwan, the Ami kept communicating with the Philippines from time to time.

Perspective from Mitochondria DNA

Mitochondria DNA are also used by many genetic studies to explore AN expansion, and some of them recruited Taiwan AN samples (Melton *et al.* 1995, 1998; Tajima *et al.* 2003; Trejaut *et al.* 2005). Melton *et al.* first studied mtDNA variation in 4 Taiwan AN populations (Ami:7, Atayal:7, Bunun:7, Paiwan:7) in 1995. They suggested that Taiwan AN populations held an ancestral position in the spread of mtDNAs throughout Southeast Asia and Oceania. In 1998, Melton *et al.* reanalyzed the same set of data and found a specific 9-base-pair deletion spread to Southeast Asia and Oceania due to the bottleneck effect in Taiwan ANs southbound expansion. They then suggested that Taiwan ANs have temporal roots in central or southern China, and have been isolated from other Asian populations in recent history.

However, Oppenheimer and Richard (2001) rechecked Melton *et al.*'s data and suggested that the so-called Polynesian motif — a mtDNA type by which Melton *et al.* considered Taiwan the first stop in AN expansion — was indeed formed in eastern Indonesia. The Polynesian motif is constructed by four SNPs in the control region and a 9-base-pair deletion in COII/tRNA region. The Polynesian motif was given the name because it reaches very high frequencies in Polynesian populations. This motif is distributed throughout the lowland populations of coastal Melanesia and the biogeographic zone of Wallacea. More importantly, it is almost absent to the west of Wallace's line. It is not found in the Philippines, Taiwan or China — all key stations along the 'express-train' route. Instead, in these regions its immediate ancestor is found with only three of the four polymorphisms, apparently breaking the train ride somewhere around Wallacea, where the final mutation in the motif, at nucleotide position 16,247, evidently occurred. This suggests that Wallacea, instead of Taiwan, might have harbored an ancient, indigenous population from which the Polynesian colonists emerged.

Tajima *et al.* (2003) studied the hyper-variable segment 1 (HVS 1) sequences of mtDNA among 20 individuals belonging to nine Taiwan AN populations. To explore phylogenetic relationships among Taiwan AN populations and other human populations, a Neighboring Joint method was adopted. The NJ tree demonstrated a tight cluster for most Taiwan AN populations, but the Ami is closely linked with other populations, popping up as an outlier in the general Taiwan AN populations. (See Figure 3.)

Trejaut *et al.* (2005) assessed mtDNA variations in 640 individuals from nine Taiwan AN populations and found a new lineage (B4a1a) totally absent in mainland China but common in Taiwan and Southeast Asia, a result backing up the theory of Polynesian migration from homeland Taiwan. However, it should be noticed that Trejaut *et al.* suggested that all Taiwan AN populations had ever moved outward.

Disagreed with this speculation, we suggest that most Taiwan AN populations should have stayed in Taiwan and only the Ami had once moved out and kept contacted with other islanders. The data attached in the paper showed that the Ami is the only group with an extremely high frequency of B4a1a (44.9%), which is otherwise either totally absent or at best rare among other Taiwan AN populations (Saisiat:0%; Bunun:0%; Paiwan:0%; Puyuma:0; Atayal:3.7%; Rukai:6%; Tsou:10%; Yami:14.1%). We hypothesize that the uneven distribution of B4a1a between the Ami and other Taiwan AN populations reflects a recent gene flow event instead of inheriting from the same origin.

Interestingly, Southeast Asian populations had higher B4a1a frequencies than general Taiwan AN populations (Moluccas:24.2%; Philippines:15.3%; Indonesia: 9.3%; Luzon:5.4%), were more likely to be the sister group with Ami. However, the distribution of B4a1a was not gradient between Ami and Southeast Asian populations, so the origin of B4a1a could be any place between Taiwan and Moluccas. The distribution of gene diversity among the Taiwan AN populations suggested the multiple migrations with most groups being isolated in Taiwan and the Ami the only possible group to move out. Compared with both Ami and other Asian populations, the lesser genetic diversity among the general Taiwan ANs suggests either that early migrations were relatively restricted in numbers, duration, and origin or that subsequent population bottleneck effects resulted in the reduction of genetic diversity.

Conclusion: the position of Taiwan in Austronesian expansion

In this paper we review the genetic evidence to clarify Taiwan's role in AN expansion. Looking into the debates between the express-train and slow-boat models, or so-called the homeland and hostland theories, some evidence have pointed to a synthetic model which may well integrate the theories of homeland and hostland. Based on the archeological evidences from Peng-hu Islands, Taiwan, southeast coast of mainland China, and Island Southeast Asia, archeologist Tsang Cheng-hwa suggests Taiwan a homeland in AN expansion, but not the only one. Tsang argues that part of AN ancestors migrated from Fujien and Guangdong provinces to Taiwan around 5,000-6,000 years ago, where these peoples stayed and never moved out to other islands later on (Tsang 1992, 1995). Yet, other AN ancestors migrated from Southeast Asia, Sunda Shelf to Borneo, and then dispersed northward to the Philippines and eastbound to other Pacific islands (Tsang 2001). This model may be called the 'dual-homeland' model, considering Taiwan not only a homeland, but also a hostland in AN expansion (Table 2).

By setting the foothold on Taiwan, two origins and three possible pathways can be derived in the above models: while the slow boat model considers Southeast Asia

the homeland of Taiwan ANs, both express-train and dual-homeland models suggest a northern origin of the Taiwan ANs. Yet, the difference between the latter two models lies in one-way or two-way migrations between Taiwan and Southeast Asia (especially the Philippines): the express-train model recommends one-way migration and the latter suggests continuing migrations between peoples in the region.

The dramatic difference of Taiwan's position in the Austronesian expansion may be caused by: (1) the archeological and linguistic evidences only applied to totally independent dimensions of human activities. While language diffusion refers to cultural impact between populations, gene diffusion is involved with mass movement of people (Cavalli-Sforza *et al.*, 1994). (2) Most genetic studies ignored the diversity of Taiwan ANs, by and large assuming one Formosan group, instead of dramatically diversified groups. Nor do the models account for later effects, such as continuing migration. Under these circumstances, Taiwan is assumed to play one role in AN expansion.

Given the evidence from both genetic and archeological studies, we assert that Taiwan AN populations had temporal root in central or south China, and then most of Taiwan AN populations (except Ami) moved to Taiwan from East Asia and remained in Taiwan for a long time. The Ami should have moved in separately, and kept contacting with other islanders while they settled in eastern Taiwan. Because the continuously gene flow with other islanders blocked its original genotypes, it is still debatable in genetic studies about the migration between the Ami and Southeast Asia.

The special role of Ami is recommended by many linguistic and archeological evidences. Along with the point made by Bellwood *et al.* (1995:99) that only one of Taiwan ANs moved out of Taiwan, Tryon (1995) clearly pointed to the diaspora of the Ami. Based on the Ami legend about their ancestral migration, Hsu (2001) disagreed with Tryon's linguistic inference. However, a new electron probe micro analysis confirmed the Philippine green-colored nephritic jade (2500-1300 BP) was indeed derived from the Fengtian (豐田) deposits in eastern Taiwan (Iizuka & Hung 2005). Taking into consideration of archeological and cultural data, it is safe to suppose a two-way contact between the AN groups in Taiwan and Southeast Asia.

The origin of the Yami seems to be less ambiguous now. They might have moved to Taiwan together with other Taiwan AN populations and started to move out to Lanyu and extend to Batan Islands only recently. This postulation finds support from archeological evidence. Tsang (2005) found the prehistoric cultures of Lanyu islands undoubtedly identical with those found at the sites of Peinan Culture (卑南) and Huagangshan Culture (花崗山) in the east coast of Taiwan. Besides, the dating of jar burials from old to new were east coast, Lanyu Islands, and Batanes Islands. These findings strongly imply that eastern Taiwan is more likely the common homeland of

the ancient inhabitants of both Batanes and Lanyu. This theory opposes the popular belief that the Yami emigrated from Batanese Islands but gains support from the studies of HLA loci (Lin et al. 2000; Chu et al. 2001), Y chromosome lineages (Capelli et al. 2001), and mtDNA lineages (Tajima et al. 2003; Trejaut et al. 2005)..

In a breakthrough paper Peter Bellwood (1991:92) has aptly suggested that “complex processes of population assimilation and interaction.....all over the Austronesian world would make any simplistic view of a south Chinese or Taiwanese origin for all modern Austronesians quite unforgivable.” To probe the credibility of each model, it requires interdisciplinary cooperation to provide more comprehensive information. In this regard, both archaeological and genetic data are equally critical.

Figure 1. Neighbor-joining tree of Taiwan AN populations, East Asians, Southeast Asians and other populations worldwide (from Chu et al. 2001).

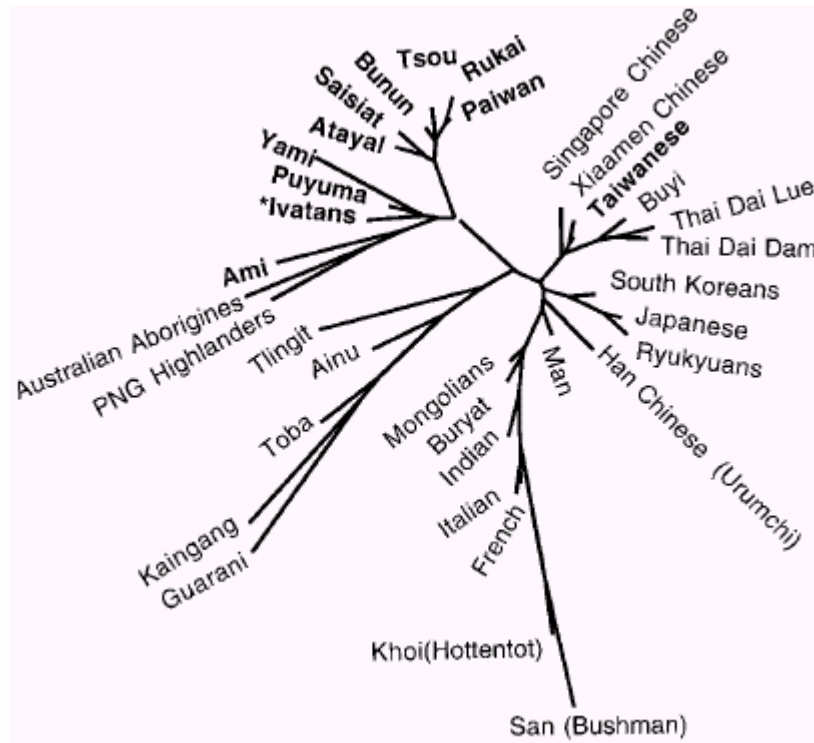


Figure 2. Phylogenies constructed by using the neighbor-joining method based on 30 microsatellites. Numbers on the branches are bootstrap values based on 500 replications. (from Chu *et al.* 1998)

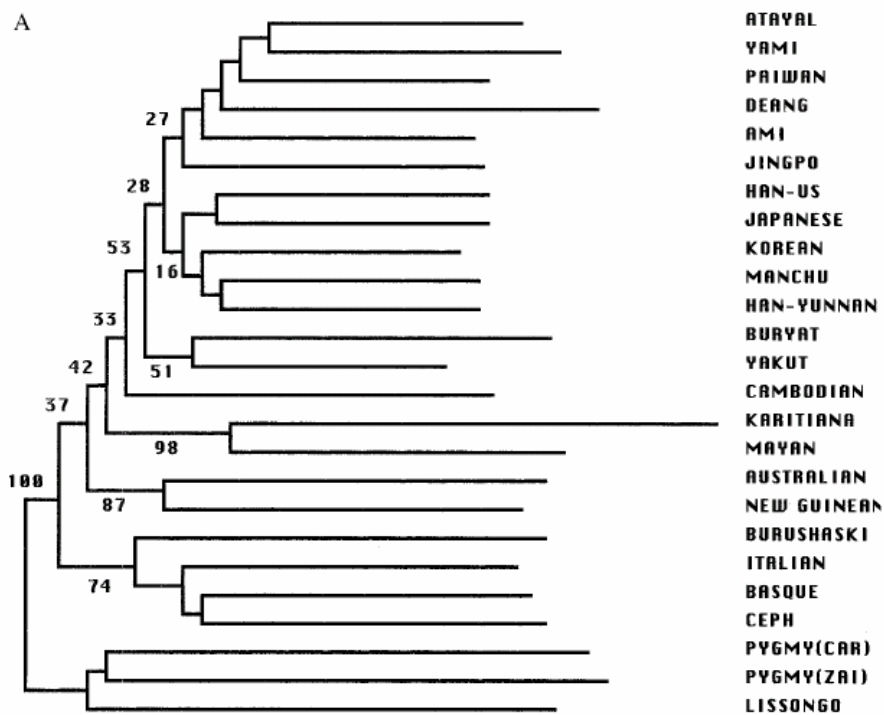


Figure 3. Neighbor-joining (NJ) tree for the nine Taiwan AN populations and other Asian and African populations (from Tajima et al. 2003). Ami showed difference with other eight populations (including Yami).

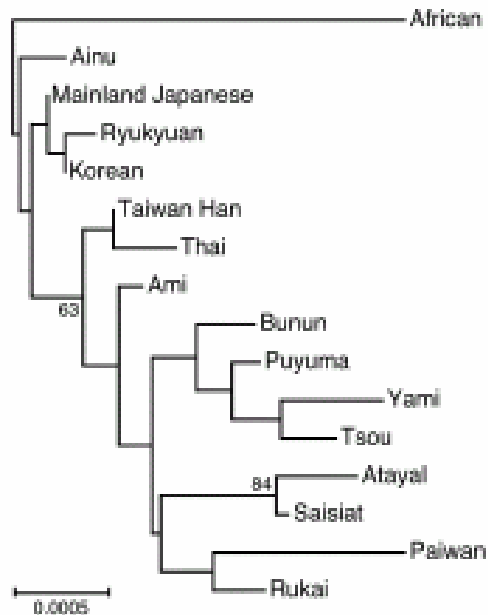


Table 1. Genetic distances by the data of Capelli *et al.* 2001

Populations	Dm^*
Ami – Philippine	0.025
Ami – Southern Chinese	0.034
Philippine – Southern Chinese	0.036
Non-Ami Taiwan – Ami	0.068
Non-Ami Taiwan – Philippine	0.073
Non-Ami Taiwan – Southern Chinese	0.087

*Nei 1978

Table 2. Taiwan’s position in different AN expansion models

Model	Origin	Migration pathway
Express-train	North	East Asia→Taiwan→Philippine
Dual-homelands	North	East Asia→Taiwan
Slow-boat/Entangled-bank	South	Southeast Asia→Philippine→Taiwan

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